

The effects of suckling on normal and delayed cycles of reproduction in the Red Kangaroo

By G. B. SHARMAN

Eingang des Ms. 23. 12. 1963

Introduction

In non-lactating female marsupials the occurrence of fertilization, followed by immediate gestation of the embryo, does not delay the onset of the following oestrus. In those marsupials in which the gestation period is considerably shorter than the length of one oestrous cycle, such as *Didelphis virginiana* (HARTMAN, 1923) and *Trichosurus vulpecula* (PILTON and SHARMAN, 1962), oestrus recurs at the expected time if the young are removed at birth. In several species of Macropodidae, such as *Setonix brachyurus* (SHARMAN, 1955), *Potorous tridactylus* (HUGHES, 1962) and the Red Kangaroo (SHARMAN and CALABY, 1964), the gestation period occupies almost the length of one oestrous cycle and oestrus is imminent at the time of parturition. Oestrus thus recurs just after the young reach the pouch (post-partum oestrus) presumably because pro-oestrus changes are initiated before the onset of the suckling stimulus. In all marsupials suckling of young in the pouch is accompanied by a lengthy period during which oestrus does not occur. This period is called the quiescent phase of lactation or, simply, the quiescent phase. It differs from seasonal anoestrus in that the ovaries and other reproductive organs respond to the removal of the suckling stimulus by resuming cyclic functions. Those marsupials in which post-partum oestrus occurs exhibit discontinuous embryonic development analogous to the delayed implantation which occurs in some eutherian mammals. If fertilization takes place at post-partum oestrus the resulting embryo assumes a dormant phase, at the blastocyst stage, and is retained as a dormant blastocyst during the quiescent phase. In these marsupials pregnancy (the interval between copulation at post-partum oestrus and parturition) is long and gestation of the embryo is interrupted by the dormant phase.

In the Red Kangaroo, *Megaleia rufa* (Desm.), the oestrous cycle averages 34 to 35 days and the gestation period is 33 days in length (SHARMAN and CALABY, 1964). Post-partum oestrus occurs, usually less than 2 days after the newborn young reaches the pouch, and a dormant blastocyst is found in the uterus of females, fertilized at post-partum oestrus, which are suckling young less than 200 days old in the pouch (SHARMAN, 1963). If the young is removed from the pouch suckling ceases and the dormant blastocyst resumes development: the young derived from it being born about 32 days after removal of the pouch young (RPY). This birth is followed by another post-partum oestrus or, if the female was not carrying a blastocyst, by a normal oestrus. Oestrus recurs at the same number of days after RPY irrespective of whether a delayed blastocyst was carried or not. The sequence of events from RPY to the next oestrus is called the delayed cycle of reproduction¹ to distinguish it from the normal reproductive cycle which follows oestrus. The delayed reproductive cycle may be divided into delayed gestation and delayed oestrus cycle according to whether a dor-

¹ The term "delayed cycle of reproduction" or "delayed (reproductive) cycle", was introduced by TYNDALE-BISCOE (1963) to describe the resumption of ovarian activity, and the features associated with it, following removal of pouch young (RPY).

mant blastocyst does or does not complete development. If the young is retained in the pouch until it leaves in the normal course of events the delayed reproductive cycle occurs coincident with the latter stages of pouch life. The dormant phase of the blastocyst gives way to renewed development when the pouch young is a little over 200 days old and subsequent vacation of the pouch, at an average age of 235 days, is immediately followed by birth of another young (SHARMAN and CALABY, 1964). The young is suckled for another 130 days, that is until it is about a year old, after it leaves the pouch. During this period the normal reproductive cycle occurs if the pouch is not occupied. It is thus evident that, although the delayed reproductive cycle occurs after RPY and cessation of lactation, some factor other than the actual production of milk must be implicated for both delayed and normal cycles may also occur during lactation.

The aim of the experiments reported below was to determine the effect of the suckling stimulus on both normal and delayed reproductive cycles. Additional suckling stimulus was provided by fostering an extra young on to females already suckling a young-at-foot. The experimental approach was suggested by chance observations on a female Red Kangaroo which, while suckling her own young-at-foot, alternately fed the young of another female kept in the same enclosure. There are four teats in the pouch but the teat to which the young attaches after birth alone produces milk and its underlying mammary gland produces all the milk for the young from birth to weaning. The female's own young and the foster-young thus shared the products of a single mammary gland and used the same teat alternately. Some initial results, in so far as they were relevant to the theme of delayed implantation, were reported earlier in a review of that subject (SHARMAN, 1963).

Methods

The results presented consist of observations on a minimum of five reproductive cycles in the female Red Kangaroo in each of the following categories:

1. Normal cycle of reproduction, suckling one young-at-foot.
2. Normal cycle of reproduction, suckling two young-at-foot.
3. Delayed cycle of reproduction, suckling one young-at-foot.
4. Delayed cycle of reproduction, suckling two young-at-foot.

The results are compared with data on the normal and delayed cycles of reproduction in non-lactating females most of which have been published elsewhere (SHARMAN, 1963; SHARMAN and CALABY, 1964; SHARMAN and PILTON, 1964). In most cases the experimental females were pregnant or carrying dormant blastocysts so that cycles of normal or delayed gestation with subsequent post-partum oestrus were studied. The gestation periods and cycles were regarded as having been significantly lengthened when they occupied a time greater by the length of two, or more, standard deviations than similar cycles in control, non-lactating, females.

Some difficulty was experienced in getting females to accept foster-young and only six females readily did so. The experiments were therefore done serially one female being used in two and two females in three experiments.

The animals were watched from a hide overlooking the enclosures and observed with binoculars. An initial watch was always done to find whether females accepted their potential foster-young. Thereafter prolonged watches were kept on some females to determine the amount of time spent suckling the young-at-foot.

Vaginal smears for the detection of oestrus and copulation were taken as reported previously (SHARMAN and CALABY, 1964).

Results

Effects of suckling on the normal cycle of reproduction

In thirteen non-lactating female Red Kangaroos forty-two intervals from oestrus to the succeeding oestrus averaged 34.64 days with a standard deviation of 2.22 days (34.64 ± 2.22 days). Twenty gestation periods in fourteen females lasted 33.00 ± 0.32 days (Fig. 1A). In five females, each observed for a single reproductive cycle while suckling one young-at-foot, the intervals between two successive oestrous periods were not different from those in non-lactating females (Fig. 1B). In another female (K32a)

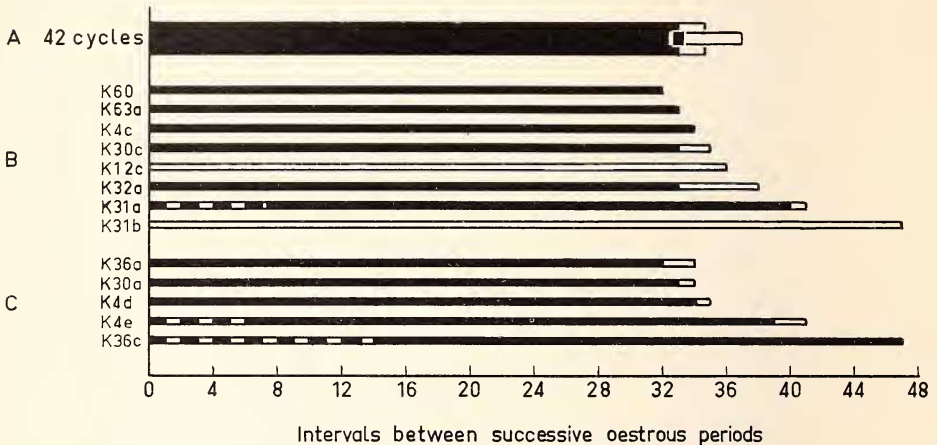


Fig. 1. Intervals between successive oestrous periods in nonlactating (control) female Red Kangaroos (A), females suckling one young-at-foot (B) and females suckling two young-at-foot (C). Black lines — continuous embryonic development, broken lines — approximate periods of dormant phase in embryo induced and maintained by suckling young-at-foot, open lines — no embryos present, bars inserted in A — standard deviations either side of mean.

the gestation period was not significantly different from that of control females but oestrus did not occur until 5 days post-partum. This was the longest interval between parturition and post-partum oestrus recorded but it is not regarded as significant. Two cycles in female K31, one lasting 41 days and one 47 days, were abnormally long. The 41-day cycle is of special significance since the interval between copulation and birth was 40 days. This differs so much from the gestation period in the control, non-lactating, females that it must be assumed that suckling of the single young-at-foot induced a short quiescent phase in the uterus accompanied by a dormant phase of about 7 days in the embryo. The 47-day cycle was over 12 days longer than the mean normal cycle length and 7 days longer than the maximum cycle length. The female copulated at oestrus but did not give birth so it is presumed that fertilization did not occur.

In three females already suckling one young-at-foot, which had another young-at-foot fostered on to them at about the time of fertilization, the lengths of the reproductive cycles were not significantly different from those in control females. Two females had significantly longer cycles than in control females. One of these (K36) was used in three successive experiments while suckling the same two young-at-foot. In the first of these (K36a) the extra suckling stimulus had no significant effect on the length of the reproductive cycle. The second experiment concerned the delayed reproductive cycle and is reported below. During the third experiment (K36c) the young were being weaned but a highly significant result was obtained. The interval from copulation to

birth showed conclusively that a dormant phase had been induced and maintained in the embryo for about 14 days of the 47-day pregnancy. In the other female in which the cycle was prolonged (K4e) the embryo presumably had a dormant phase of about 6 days.

Effects of suckling on the delayed cycle of reproduction

In ten non-lactating females thirteen intervals from RPY to the succeeding oestrus were 34.46 ± 1.92 days. In seven of these females the delayed gestation period was 31.64 ± 0.65 days (Fig. 2A). There was no evidence that suckling one young-at-foot had any effect on the length of the delayed reproductive cycle (Fig. 2B). In one female (K12a) the interval from RPY to the following oestrus was 38 days but this falls short of the minimum interval accepted as significantly different.

All six females suckling two young-at-foot (Fig. 2C) were carrying a dormant blastocyst in the uterus when the pouch young were removed. In five of these the interval RPY to birth was significantly longer than in control females (Fig. 2C). The interval RPY to the next oestrus was longer than the mean for control non-lactating females in all six experimental females and in three of them (K4b, K30b, K36b) the difference from controls was highly significant. It must be concluded that the blastocysts of five of the above experimental females remained in the dormant phase for between 3 and 22 days longer after RPY than did those of control non-lactating females and females suckling one young-at-foot.

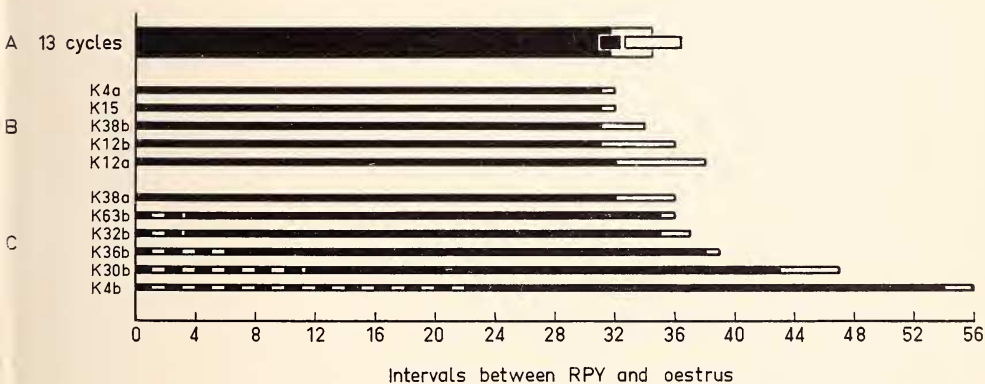


Fig. 2. Intervals between removal of pouch young (RPY) and the next oestrus in non-lactating (control) female Red Kangaroos (A), females suckling one young-at-foot (B) and females suckling two young-at-foot (C). Black lines — continuous embryonic development, broken lines — approximate periods of continued dormant phase of embryo maintained by suckling young-at-foot, bars inserted in A — standard deviations either side of mean.

The amount suckling in relation to occurrence of parturition and return to oestrus

Observations on the habits of the pouch young suggested that the stimulus causing withholding of the mother's reproductive cycles might be tactile and received via the teat. The young during the early stages of pouch life, when reproductive cycles were withheld, were suckled continuously and could not regain the teat if removed before the age of 6 weeks. Later young were able to take the teat back into their mouths but were seldom found free of the teat before the age of about 5 months. On the other

Table 1
Effects of suckling one and two young-at-foot on subsequent parturition and oestrus in Red Kangaroos

No. of female	Ages of young (days)		No. of hours observed	Minutes of suckling			Type of cycle	Effects of suckling on subsequent parturition and oestrus	
	Own young	Foster-young		Own young	Foster-young	Per day		Occurrence of parturition	Occurrence of oestrus
K 60	255	—	13,5	44	—	78	normal	when expected	when expected
K 31 (a)	255	—	15,5	31	—	48	normal	late	late
K 31 (b)	269	—	96	203	—	51	normal	no young born	late
K 30 (c)	288	—	13,5	38	—	68	normal	when expected	when expected
All females suckling 1 young									
			138,5	316	—	53			
All females suckling 2 young									
K 4 (e)	259	245	22,5	86	55	150	normal	late	late
K 63 (b)	309	309	15,5	27	31	90	delayed	late	when expected
K 36 (b)	322	315	78	192	83	85	delayed	late	late
			116	305	169	98			

hand the pouch young present when the delayed reproductive cycle occurred apparently frequently released the teat as they were seen protruding their heads from the pouch to feed from the ground or leaving the pouch entirely (SHARMAN and CALABY, 1964).

Theoretically it was to be expected that if reproductive cycles resumed in response to a lowered suckling stimulus, as they did during the terminal stages of pouch feeding, then the cycles which occurred as soon as the young left the pouch should have been of normal length. Six of the eight cycles shown in Fig. 1B were the first which occurred after termination of pouch feeding. Four were of normal length but two cycles in one female (K 31 a, b) were lengthened by a significant amount. Observations on the habits of the young, just after they left the pouch permanently, showed that they frequently attempted to regain the pouch but were restrained from doing so by their mothers (SHARMAN and CALABY, 1964). In these cases they spent long periods with their heads in the pouch during which time they may have grasped the teat. It is also possible that the young, subjected permanently for the first time to the cooler environment outside the pouch, fed more frequently than they did during the ter-

minal stages of pouch life. This would result in a greater suckling stimulus being exerted: at least during the initial stages of life outside the pouch.

A number of females suckling one or two young-at-foot were watched continuously for varying periods and the amounts of time spent suckling were recorded (Table 1). It was at once apparent that females feeding two young-at-foot spent nearly twice as much time suckling as did females with a single young-at-foot. The relationship between amount of suckling and interruption or resumption of the reproductive cycle is, however, not so obvious. Thus, in female K31, 48 and 51 minutes of suckling per day were associated with lengthening of the interval between successive oestrous periods and 48 minutes per day with inducing and maintaining a short dormant phase in the embryo. In two other females (K60, K30c) a greater amount of suckling apparently had no effect on the length of the cycle or on pregnancy. However, although the watches were done during the relevant cycles, they were not necessarily done at the critical period of the cycle when the suckling stimulus exerted its effect. This period could not be ascertained since no evidence of its occurrence was available until the females gave birth or returned to oestrus. The figures in Table 1 are thus to be regarded as no more than a guide to the amount of suckling which occurred at the critical period.

The most conclusive evidence about the effect of the suckling stimulus on the reproductive cycle came from the females from which pouch young were removed while they were suckling two young-at-foot (Fig. 2C). In one of these females (K38a) the suckling of two young-at-foot was without effect on the delayed reproductive cycle; in three (K32b, K36b, K63b) the delayed cycle began while two young were being suckled but in two others (K4b, K30b) the delayed cycle was only initiated when one of the suckling young-at-foot was removed. The interval from removal of the young-at-foot to completion of the delayed cycle was approximately the same (31–32 days) as from RPY to the completion of the cycle in the control females.

The two intervals between successive oestrous periods with intervening pregnancies which were observed in the same female (K36a, c) while suckling the same two young-at-foot call for some comment. Parturition and return to oestrus occurred when expected in the first cycle but were delayed significantly in a subsequent cycle when the young were much older and were being weaned (Fig. 1C). During this, latter, cycle one of the young frequently grasped the teat for periods of 10 minutes or more but when the female's pouch was examined it was found that no milk could be expressed from the teat and that the mammary gland was regressing. This was in contrast to the condition in other females suckling young-at-foot in which milk could usually be readily expressed. No watch was done to observe the amount of time the young spent sucking the dry teat as the significance of the observation was only realised after completion of the cycle. This cycle is, however, of particular significance because it appears likely that the suckling stimulus, in the absence of lactation, induced a quiescent phase in the uterus lasting some 14 days and a corresponding period of dormancy in the blastocyst.

Discussion

Delayed implantation in the Red Kangaroo is of the type usually referred to as lactation controlled delayed implantation. This description is adequate in so far as the delayed cycle of reproduction is initiated following removal of the pouch young and cessation of lactation. However, the delayed cycle also occurs during the seventh and eighth months of the 12-month lactation period. It therefore follows that, in these cases, the delayed cycle does not begin in response to the cessation of lactation or to the imminent cessation of lactation. The quiescent phase of lactation with asso-

ciated arrested development of the embryo is initiated during the early part of lactation while a small young is suckled continuously in the pouch but the normal reproductive cycle may, as has been shown above, occur during the latter part of lactation. It is thus much more likely that the amount of suckling stimulus which the female receives at various phases of the lactation period is of paramount importance in determining whether the normal reproductive cycle shall be interrupted or whether the delayed cycle shall be initiated. The experiments reported above have shown that in some females the normal cycle is interrupted and a quiescent phase of lactation, with associated dormant phase of the embryo is induced by increasing the suckling stimulus. It has also been shown that the stimulus of suckling of young, outside the pouch, is capable of prolonging the quiescent phase of lactation and dormant phase of the embryo.

Two other factors could be of importance in determining the time of onset of the delayed cycle of reproduction: 1. Temporary or permanent vacation of the pouch. 2. Fall in milk yield. Temporary emergence from the pouch first occurs when the young are less than 190 days old and permanent emergence at the average age of 235 days — that is a few days before the completion of the delayed cycle (SHARMAN and CALABY, 1964) but the delayed cycle apparently begins when the young are a little over 200 days old. Precise data on this point are difficult to obtain but assuming that the delayed cycle, once initiated, proceeds at the same rate in lactating females as it does in females from which the pouch young are removed then it must begin about 30 days before the young leaves the pouch. This is in agreement with the massive amount of data obtained from Red Kangaroos taken in the field. The onset of the delayed cycle can hardly occur in response to a fall in milk yield since it takes place when the young is actively growing and when it is increasing rapidly in weight. From the age of 200 days to the age of 220 days, during which period the delayed cycle is resumed, the pouch young increase from about 2.5 to 3.5 kg in weight which is not the expected result of a fall in milk yield. Furthermore removal of young from the pouches of females which were suckling two young-at-foot must have been accompanied by a fall in milk yield yet under these circumstances the quiescent phase of lactation with associated dormant blastocyst continued in five of six females (Fig. 2C).

The importance of the suckling stimulus in marsupial reproduction was demonstrated by SHARMAN (1962) and SHARMAN and CALABY (1964) who transferred newborn young *Trichosurus vulpecula* and *Megaleia rufa* to the pouches or teats of non-lactating, non-mated or virgin females of each of these species at the appropriate number of days after oestrus. The suckling stimulus exerted by the young induced the onset of lactation without the prior occurrence of pregnancy and oestrous cycles were withheld while the foster-young were suckled in the pouch. SHARMAN and CALABY (1964) were unable to demonstrate any behavioural differences between pregnant and non-mated female Red Kangaroos at the same number of days after oestrus except that pregnant females repeatedly cleaned their pouches just before giving birth. Other authors (HILL and O'DONOGHUE, 1913; HARTMAN, 1923; SHARMAN, 1955; PILTON and SHARMAN, 1962) have drawn attention to the remarkable resemblances of post-oestrous changes in pregnant females to those of non-mated females in various species of marsupials. It is apparent, that whereas in polyoestrous eutherian mammals hormones produced by the embryonic membranes modify the reproductive cycle and prevent the recurrence of oestrus during pregnancy, no such mechanism has yet been demonstrated in any marsupial. In those marsupials which do not have a seasonal anoestrous period, such as the Red Kangaroo, the reproductive cycle is continuous except when interrupted by the quiescent phase of lactation.

OWEN (1839—47) determined the gestation period (interval from mating to birth)

of a lactating female Great Grey Kangaroo as 38–39 days. HEDIGER (1958) stated that K. H. WINKELSTRÄTER and E. CRISTEN in Zurich Zoo found gestation periods of 30 and 46 days in the same species and later, in the same paper, stated that a young was born on the forty-sixth day after mating in a lactating female Great Grey Kangaroo. However the dates quoted by HEDIGER show that the „gestation period“ was actually 57 days. In non-lactating Great Grey Kangaroos Miss PHYLLIS PILTON (pers. comm.) found the gestation period was about 30 days and in the C.S.I.R.O. Division of Wildlife Research four gestation periods in three non-lactating females were 33 days 6 hours to 34 days 6 hours, 33 days 18 hours to 34 days 10 hours, 34 days to 34 days 17 hours and 34 days to 34 days 20 hours. It is apparent that, although the Great Grey Kangaroo does not have the same type of lactation controlled delayed implantation as occurs in the Red Kangaroo and other marsupials (SHARMAN, 1963), intervals between mating and birth in lactating females may be an unreliable guide to the gestation period. HEDIGER (1958) stated that exact gestation periods in kangaroos and other marsupials are difficult to determine because ovulation occurs several days after mating and spermatozoa can remain active in the oviduct for long periods. This may be true of the marsupial *Dasyurus viverrinus*, but HILL and O'DONOGHUE's (1913) work on this species has not been repeated and confirmed. Delayed ovulation and storage of spermatozoa do not occur in *Didelphis* (HARTMAN, 1923), *Setonix* (SHARMAN, 1955) or *Trichosurus* (PILTON and SHARMAN, 1962) and gestation periods in non-lactating females of these species can be determined with considerable accuracy. In the Red Kangaroo the intervals between mating and birth in some lactating females (Table 2) are not true gestation periods since they include

Table 2

Intervals from mating to birth and intervals from removal of pouch young (RPY) to birth in seven female Red Kangaroos subjected to different levels of suckling stimulus

No. of female	K 4	K 30	K 31	K 32	K 36	K 38	K 63
<i>Intervals from mating to birth</i>							
Non-suckling	33	—	—	33	—	—	33
Suckling 1 young	34	33	40	33	—	—	33
Suckling 2 young	34,39	33	—	—	32,47	—	—
<i>Intervals from RPY to birth</i>							
Non-suckling	32	32	—	—	—	32	—
Suckling 1 young	31	—	—	—	—	31	—
Suckling 2 young	54	43	—	35	38	32	35

a period of arrested development of the embryo. However, in thirteen non-lactating female Red Kangaroos one gestation period was 32 days, one was 34 days and eighteen were 33 days in length (SHARMAN and CALABY, 1964). The true gestation period, as in the species above, can therefore be determined with precision.

Perhaps failure to recognise the importance of the suckling stimulus accounts for the inaccuracy of some of the marsupial gestation periods given in International Zoo Year Book Vol. 1 (JARVIS and MORRIS, 1959). The list is incomplete and at least half of the figures given are wrong.

The occurrence of lactation controlled delayed implantation in marsupials was reported in 1954 (SHARMAN, 1954) and numerous papers have since appeared indicating that it is of widespread occurrence among kangaroo-like marsupials. Records of birth in captive female marsupials after long isolation from males, such as those reported by CARSON (1912) in the Red Kangaroo and, recently, by HEDIGER (1958) in Bennett's Wallaby, are readily explained in terms of the occurrence of delayed implantation.

I am indebted to Miss PAT BERGER, Mr. JOHN LIBKE and Mr. JAMES MERCHANT who helped with animal maintenance, handling and watching. The interest, assistance and advice on the manuscript given by my colleague Mr. J. H. CALABY is gratefully acknowledged.

Summary

In non-lactating female Red Kangaroos the oestrous cycle lasted about 35 days and the gestation period was about 33 days. Gestation did not interrupt the oestrous cycle. Postpartum oestrus, at which copulation and fertilization took place if the female was with a male, occurred just after parturition. Recurring reproductive cycles were replaced by the quiescent phase of lactation for up to about 200 days while the young were suckled in the pouch. If fertilization occurred at postpartum oestrus a dormant blastocyst was carried in the uterus during the quiescent phase of lactation. The delayed cycle of reproduction during which the hitherto dormant blastocyst, if present, completed development occurred following removal of young less than 200 days old from the pouch. If the young were retained in the pouch until they emerged in the normal course of events the delayed cycle of reproduction occurred coincident with the last month of pouch life and was completed a day or two after the young permanently left the pouch. Suckling of the young occupied one year: they were suckled for about 235 days in the pouch and for a further 130 days after leaving the pouch. The delayed cycle of reproduction could thus occur during, and long before the cessation of, lactation. Normal cycles of reproduction occurred during lactation if the pouch was not occupied.

The lengths of normal and delayed cycles of reproduction in females suckling one and two young-at-foot were compared with those in control, non-lactating, females. The results were as follows:

Normal cycle of reproduction

Females suckling one young-at-foot. Six cycles not significantly different from those of controls; two cycles significantly longer than in controls in one of which a dormant phase of about 7 days occurred in the embryo. Total: 8 cycles.

Females suckling two young-at-foot. Three cycles not significantly different from those of control females; two cycles significantly longer than in control females which included dormant periods of 6 and 14 days in the embryos. Total: 5 cycles.

Delayed cycle of reproduction

Females suckling one young-at-foot. No effect of suckling. Total: 5 cycles.

Females suckling two young-at-foot. One cycle not significantly different from those of control females. Five cycles longer than those of control females in which the dormant periods of the blastocysts were extended by 3, 3, 6, 11 and 22 days. In the two latter cycles resumption of development of the dormant blastocysts did not occur until removal of one of the suckling young-at-foot. Total: 6 cycles.

Observations showed that females with two young-at-foot suckled their young for about twice the length of time that females suckled a single young-at-foot. It was concluded that the suckling stimulus exerted by one or two young-at-foot could induce and maintain the quiescent phase of lactation and the associated dormant phase in the embryo. Available evidence suggested that the stimulus causing onset of the quiescent phase was tactile and received via the teat and that the delayed cycle of reproduction occurred, or the interrupted normal cycle was resumed, when the suckling stimulus was lessened.

It is suggested that some published gestation periods of marsupials owe their error to the failure of observers to appreciate the significance of concurrent suckling. Reported cases of female marsupials giving birth after long isolation from males can readily be explained as due to the occurrence of the delayed cycle of reproduction.

Zusammenfassung

Bei nichtsäugenden ♀♀ des Roten Riesenkänguruhs dauert der Oestrus-Cyclus rund 35 Tage, die Trächtigkeit rund 33 Tage. Trächtigkeit unterbricht den Cyclus nicht. Postpartum-Oestrus, bei dem Begattung und Befruchtung stattfanden, erfolgten unmittelbar nach der Geburt. Wiederkehr des Oestrus wurde durch eine Latenz während der Laktation bis zu 200 Tagen verhindert, während welcher das Junge im Beutel gesäugt wurde. Wenn beim Postpartum-Oestrus Befruchtung erfolgt war, enthält der Uterus während dieser Latenzperiode eine ruhende Blastocyste. Der verzögerte Cyclus der Fortpflanzung, während der die bisher ruhende Blastocyste (wenn sie vorhanden ist) ihre Entwicklung vollendet, tritt auf, wenn das Junge früher als 200 Tage nach der Geburt aus dem Beutel entfernt wird. Wenn die Jungen jedoch so lange im Beutel bleiben, bis sie ihn normalerweise verlassen hätten, fällt der verzögerte Cyclus der Fortpflanzung mit dem letzten Monat des Beutellebens zusammen und ist vollendet ein oder zwei Tage nachdem die Jungen den Beutel endgültig verlassen haben. Das Säugen dauert ein volles Jahr: die Jungen werden rund 235 Tage lang im Beutel und noch weitere 130 Tage bei Fuß gesäugt.

Der verzögerte Cyclus der Fortpflanzung kann also während und auch lange vor Beendigung der Laktation auftreten. Normaler Cyclus der Fortpflanzung tritt auf, wenn kein Junges im Beutel ist. Die Länge von normalen und verzögerten Cyclen der Fortpflanzung bei säugenden ♀♀ mit einem bzw. zwei Jungen bei Fuß wurde mit solchen bei nicht säugenden Kontroll-♀♀ verglichen. Die Ergebnisse waren:

Normaler Cyclus der Fortpflanzung

bei ♀♀, die 1 Junges bei Fuß säugten: 6 Cyclen waren nicht besonders verschieden von den Kontroll-♀♀. Zwei Cyclen waren bedeutend länger; bei einem davon machte der Embryo eine Ruhepause von etwa 7 Tagen durch. Im ganzen 8 Cyclen.

Bei ♀♀, die 2 Junge bei Fuß säugten: 3 Cyclen nicht besonders verschieden von den Kontroll-♀♀; 2 Cyclen bedeutend länger als bei den Kontroll-♀♀ mit Ruheperioden des Embryos von 6 und 14 Tagen. Im ganzen 5 Cyclen.

Verzögerter Cyclus der Fortpflanzung

bei ♀♀, die ein Junges bei Fuß säugten, ergab sich kein Einfluß des Säugens. Im ganzen 5 Cyclen.

Bei ♀♀, die 2 Junge bei Fuß säugten, war 1 Cyclus nicht sehr verschieden von den Kontroll-♀♀. 5 Cyclen waren länger als bei den Kontroll-♀♀, bei denen die Ruhezeit der Blastocyste resp. 3, 3, 6, 11 und 22 Tage betrug. In letzteren beiden setzte die Weiterentwicklung nicht ein, bevor nicht eines der Jungen weggenommen wurde. Im ganzen 6 Cyclen.

Die Beobachtungen zeigten, daß ♀♀ mit 2 Jungen bei Fuß ihre Jungen doppelt so lange säugen, wie sie ein einziges gesäugt haben würden. Daraus wurde geschlossen, daß der Saugestimulus, von einem oder zwei Jungen bei Fuß ausgelöst, sowohl die Ruhephase während der Laktation, als auch die damit gleichlaufende Ruhephase des Embryos einleitet und erhält. Die bisherige Erfahrung läßt annehmen, daß der Stimulus, der den Beginn der Ruhephase bewirkt, tactil ist und über die Zitze empfangen wird, und daß der verzögerte Cyclus der Fortpflanzung auftritt, oder der unterbrochene normale Cyclus wieder aufgenommen wird, wenn der Saugreiz sich vermindert.

Einige von anderer Seite veröffentlichte Daten über Trächtigkeitsdauern von Beuteltieren enthalten offenbar Fehler, da die betreffenden Autoren die Bedeutung gleichlaufenden Säugens nicht beachteten. Mitgeteilte Fälle, daß ♀ Beuteltiere auch nach langer Isolierung vom ♂ waren, kann ohne weiteres durch das Auftreten des verzögerten Fortpflanzungs-Cyclus erklärt werden.

Literature

- CARSON, R. D. (1912): Retarded development in a red kangaroo; Proc. zool. Soc. Lond. 1912, 234-235. — HARTMAN, C. G. (1923): The oestrous cycle in the opossum; Am. J. Anat. 32, 353-421. — HEDJGER, H. (1958): Verhalten der Beuteltiere (Marsupialia); Handbuch Zool. 8, 18 Lief 10(9), 1-28. — HILL, J. P., and O'DONOGHUE, C. H. (1913): The reproductive cycle in the marsupial *Dasyurus viverrinus*. Quart. J. micr. Sci. 59, 133-174. — HUGHES, R. L. (1962): Reproduction in the macropod marsupial *Potorous tridactylus* (Kerr); Aust. J. Zool. 10, 193-224. — MORRIS, D., and JARVIS, C. (Eds.) (1959): The International Zoo Year Book, Vol. 1; London. — OWEN, R. (1839-47): Marsupialia; In: The Cyclopaedia of Anatomy and Physiology, Vol. 3 (ed. R. B. Todd), London. — PILTON, P. E., and SHARMAN, G. B. (1962): Reproduction in the marsupial *Trichosurus vulpecula*. J. Endocrin. 25, 119-136. — SHARMAN, G. B. (1954): Reproduction in marsupials; Nature, Lond. 173, 302-303. — SHARMAN, G. B. (1955): Studies on marsupial reproduction. 3. Normal and delayed pregnancy in *Setonix brachyurus*; Aust. J. Zool. 3, 56-70. — SHARMAN, G. B. (1962): The initiation and maintenance

of lactation in the marsupial *Trichosurus vulpecula*; J. Endocrin. 25, 375–385. — SHARMAN, G. B. (1963): Delayed implantation in marsupials; In: Delayed implantation (ed. A. C. Enders), Chicago. — SHARMAN, G. B., and CALABY, J. H. (1964): Reproductive behaviour in the red kangaroo in captivity; C. S. I. R. O. Wildl. Res. 9 (in press). — SHARMAN, G. B., and PILTON, P. E. (1964): The life history and reproduction of the red kangaroo (*Megaleia rufa*). Proc. zool. Soc. Lond. 142 (in press). — TYNDALE-BISCOE, C. H. (1963): The rule of the corpus luteum in the delayed implantation of marsupials; In: Delayed implantation (ed. A. C. Enders), Chicago.

Author's address: Dr. G. B. SHARMAN, C. S. I. R. O. Division of Wildlife Research, Canberra, A. C. T., Australia

Zwillingsgeburt beim Großohr-Hirsch, *Odocoileus hemionus* Raf.

VON GÜNTER VOSS

Aus dem Assiniboine Park Zoo, Winnipeg, Manitoba, Canada
Direktor: Dr. Günter Voss

Eingang des Ms. 19. 8. 1963

Der Großohr-Hirsch heißt in Nordamerika Mule Deer, Maultier-Hirsch. Zweifellos haben ihm die großen Ohren diesen Namen eingebracht, die um ein Viertel länger sind als bei seinem Verwandten, dem Weißwedel-Hirsch.

Das Verbreitungsgebiet des Großohr-Hirsches umfaßt die nordamerikanischen Rocky Mountains, außer in ihrem arktischen Teil und außer Alaska, und deren östliches Vorland. Am weitesten reicht die Verbreitung des Großohr-Hirsches nach Osten in Nord-Dakota und Südwest-Manitoba. Hier nennt man ihn volkstümlich „jumping deer“ wegen einer eigentümlichen Bewegungsart, die aus einer Folge hoher Sprünge besteht.

In jüngster Zeit vollzieht sich eine Einschränkung des Lebensraumes des Großohr-Hirsches, die indirekt durch intensivere Urbarmachung des Westens von Nordamerika bedingt zu sein scheint. Eindringling in den früheren Großohr-Hirsch-Lebensraum ist die östliche Art telemetakarpaler nordamerikanischer Hirsche, der Weißwedel-Hirsch, auch immer noch „Virginia-Hirsch“ genannt. Dies haben mir mehrere Wildkenner und Zoologen unabhängig berichtet: C. I. TILLENUS, Ottawa, E. F. BOSSENMAIER, Winnipeg, A. F. OEMING, Ardrossan, und andere. Ich sah selbst „im Herzen“ des Großohr-Hirsch-Verbreitungsgebietes, im Kootenay National Park am Oberlauf des Kootenay-Flusses, etwa 160 km westsüdwestlich von Calgary, im Sommer 1962 Weißwedel-Hirsche. Der Weißwedel-Hirsch wird gern als typischer Kulturfolger bezeichnet. Zumindest im mittleren und westlichen Kanada trifft man ihn tatsächlich viel zahlreicher in der Nähe landwirtschaftlich genutzter Flächen als in Prärie, Klüften, Ödland, Bruch und Urwald. Hierin unterscheiden sich anscheinend die Weißwedel- von den Großohr-Hirschen.

Ganz so schematisch, wie es die Ausdrücke „Kulturflüchter“ und „Kulturfolger“ wahrhaben wollen, lassen sich allerdings Großohr- und Weißwedel-Hirsche doch nicht behandeln. Um den idyllischen Höhenkurort Jasper herum (etwa 330 km westsüdwestlich von Edmonton) kommen Großohr-Hirsche ganz nahe an Wanderwege und sogar Straßen und Waldhotels heran und lassen sich von Kurgästen füttern. In Banff (140 km westnordwestlich von Calgary) äsen Großohr-Hirsche so regelmäßig in Randbezirken des Ortes, daß die Grundstücksbesitzer hohe Drahtzäune um ihre Hausgärten gezogen haben.